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AN OVERVIEW OF FORAGING THEORY

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One of the most active areas of ecological research concerns predation and herbivory. Of interest is how an individual allocates its time and energy in search of food. Animal nutritional requirements vary greatly, not only in quantity, but also in quality, and it is not my aim here to review the variety of feeding mechanisms employed, nor the physiology of alimentary systems and digestion. See Jennings (1965) for a review of these. Rather, the questions of ecological interest are, given certain physiological needs and constraints on feeding, what complex of behavioral traits are employed to meet these needs. My discussion will concern only animals, but analogous questions for plants were mentioned in the lecture on biophysical ecology concerning leaf sizes which maximize photosynthetic gains. Without the behavioral repertoire available to animals, plant respond to the problem of "foraging" for light, water, and nutrients through phenotypically plastic growth forms (Bradshaw, 1965).

The approach I describe for analyzing adaptive feeding strategies is the a priori methodology mentioned in the biophysics lecture. Several reviews of foraging theory have appeared (Schoener, 1971; Pyke et al., 1977; Krebs and Davies, 1981; Townsend & Hughes, 1981), and my purpose here is not to give a complete review, but rather an introduction to the various theoretical questions which have been attacked. I would like to emphasize that this area is one in which models have proliferated at a very rapid rate, with relatively few experimental tests which can readily discriminate between models. I will mention a few of the tests which have been done, but will not attempt by any means to be comprehensive. Pyke et al. (1977) give a good review of model testing, but there has been much more done since their paper appeared. Readers should consult volumes of the American Naturalist and the Journal of Animal Ecology for more recent work.

The approach taken in foraging theory is essentially an optimization one (Maynard Smith, 1978). The technique is threefold. First a set of possible behavioral responses of the animal must be delineated, this being the phenotype set of Maynard Smith. The phenotype set specifies the range of responses which it is assumed are available to a population through the action of evolution. Secondly, the state equations of the system must be described. These constraints describe how organism response is coupled to the environment and include responses which are not subject to change via evolution. For example, in most foraging models it is assumed that the perceptual abilities of individuals are inflexible and thus the distances over which a prey item can be located are fixed by the state

equations. Lastly, a fitness criterion must be defined, giving a function over the phenotype set which assigns a fitness to each phenotype. It is assumed that evolution acts to maximize this fitness, and the predicted phenotypes from this maximization may then be compared to those actually observed in the field. As mentioned in the biophysics lecture, this approach has its weaknesses. It ignores the underlying genetics of the evolutionary process and thus is subject to many of the criticisms of optimality thinking in ecology (Oster & Wilson, 1978). It is best in using it to carefully describe the particular assumptions made, so that when tests are done it will be clear which hypotheses of the model are being tested. Unfortunately, for foraging applications, often many more assumptions need to be included than are amenable to observational testing, but the models still provide one of the few means available to conceptualize the outcomes of different resource utilization patterns by animals (Townsend & Hughes, 1981).

The procedure is thus to first construct a model for how an organism feeds in terms of the habitat (such as patchy or not), the abundance of potential prey items and their relative values to the predator, and particular behaviors of the predator such as flight ability. Included within the model are variables which are assumed to be under evolutionary control, such as fraction of each prey type attacked, or time in a day spent actively foraging. These control variables specify the foraging strategy. The model choice may depend upon the currency used to describe the system; often some measure of energy gain to the forager is used. The costs and benefits of the range of potential foraging strategies are computed in terms of this common currency. An optimal strategy is then determined based upon a given optimization criterion such as maximizing net energy gain per unit time, or total energy gain in a day. This approach has been applied to problems such as determining what food types to eat, which types of patch to feed in, how much time to spend in different patches, and what patterns and speed of movement to use (Pyke et al., 1977).

One of the most confusing aspects of the literature on foraging theory is the number of different optimization criteria that have been used. Those most frequently applied include the rate of net energy gain (Pulliam, 1974; Charnov, 1976; Oaten, 1977; De Benedictus et al., 1978; Waddington and Holden, 1979), optimal use of time (Katz, 1974; De Benedictus et al., 1978; Craig et al., 1979; Pyke, 1979; Hixon, 1980), and total food uptake or reward (Oster, 1976; Craig et al., 1979; Pyke; 1979; Hixon, 1980). Other criteria suggested include energy gain efficiency (De Benedictus et al., 1978; Pyke, 1979), survivorship (Caraco, 1979), and utility (Caraco, 1980). Though many of these studies site data to indicate they have made a proper choice of criteria, arguments have arisen over the matter (De Benedictus et al, 1978; Pyke, 1979; Sih, 1979). Also subject to debate is what constraints should be included when carrying out the optimization procedure (Oaten, 1977; Pyke, 1979). Below I give examples of how some of these criteria are applied.

A few studies have attempted to compare model results using a number of different optimization criteria with experimental data, though the results are somewhat conflicting. De Benedictus et al. (1978) compare four different criteria for meal size in hummingbirds and find that the rate of net energy gain and energy gain efficiency are optimized and not the use of time or total net energy gain. Pyke (1979), in a comparison of four criteria in a model of sunbird foraging, determines that daily energy cost is minimized while net energy gain and energy gain efficiency are very poor criteria to use. Hixon (1980) compares energy maximization strategies with optimal use of time strategies, but concludes that the available data is not adequate to test the predictions of the two approaches. Clearly, this is one area in which further experimentation is needed.

My procedure in what follows is to first develop the simplest deterministic foraging models for the cases of optimal diet and patch choice, following Townsend & Hughes (1981). I will then cover some detailed models to give an indication how the simpler models can be easily elaborated, with sometimes contradictory results. Finally, I will mention some problems which I feel have been relatively unexplored theoretically.

Diet Choice

Here, the abundance and distribution of prey items in the environment are assumed fixed. Each prey item, i, has a fixed energy content c_i, which is utilizable by the predator, and also has a fixed handling time h_i, which represents the amount of time necessary for the predator to actually consume the prey-item once it has been located. The density of prey type i is λ_i. The control parameters which specify the foraging strategy are the fractions, p_i, of prey type i which are actually attacked, given that a type i prey is encountered. For example, if there are only two prey types with $p_1 = 1$ and $p_2 = 0$, then the predator is a "specialist" on prey type 1 and ignores prey type 2. If $p_1 > 0$ and $p_2 > 0$, the predator is a "generalist" in the sense that it will attack both prey types. If $p_1 > p_2$, the predator is said to "prefer" prey type 1 over type 2. The optimization criterion considered is the mean rate of energy gain per unit time, and the optimal strategy will be that set of p_i's which maximizes this.

The time required for a predator to locate a prey item is assumed exponential,

$$P[T_s \le t] = 1 - e^{-\lambda t} \qquad (1)$$

where T_s is the random variable for time since start of the search when the prey is located, and $\lambda = (\lambda_1 + \lambda_2 + \cdots + \lambda_n)a$ is the product of the density of prey $(\lambda_1 + \cdots + \lambda_n)$ and the area searched per unit time by the predator (a). This will hold for the situation when prey items are distributed according to a Poisson distribution in 2-space, and the predator moves at constant speed, searching a constant area per unit time, with no overlap with area already searched. In the above the phenotype set is the set of attack probabilities, $0 \le p_i \le 1$. The state constraints are that the predator travels at a constant speed, has a fixed set of potential prey items, $i = 1, 2, \ldots, n$, and has a fixed efficiency for handling each prey type, since the h_i's are fixed. The model analysis follows Pulliam (1974).

Consider a single prey arrival. The mean time for one prey arrival to occur is

$$E[T_s] = \frac{1}{\lambda} \qquad (2)$$

where $E[\cdot]$ is expectation. The total time from the start of the search for the first prey item to the start of the search for the second prey item is $T = T_s + T_p$, where T_p is the random variable for pursuit or handling time. By the law of total probability

$$E[T_p] = \sum_{i=1}^{n} h_i \, P\left[\begin{matrix}\text{1st prey arrival}\\ \text{is attacked}\end{matrix} \,\middle|\, \begin{matrix}\text{1st prey arrival}\\ \text{is type } i\end{matrix}\right] P\left[\begin{matrix}\text{1st prey arrival}\\ \text{is type } i\end{matrix}\right]$$

$$= \sum_{i=1}^{n} h_i \, p_i \, \frac{\lambda_i}{\lambda} \qquad (3)$$

so

$$E[T] = \frac{1}{\lambda}\left(1 + \sum_{i=1}^{n} h_i \, p_i \, \lambda_i\right). \qquad (4)$$

Similarly, the mean caloric gain C, from the first prey arrival is

$$E[C] = \frac{1}{\lambda} \sum_{i=1}^{n} c_i \, p_i \, \lambda_i \qquad (5)$$

and the fitness criterion is

$$F = \frac{E[C]}{E[T]} = \frac{\sum_{i=1}^{n} c_i p_i \lambda_i}{1 + \sum_{i=1}^{n} h_i p_i \lambda_i} . \qquad (6)$$

The problem is then to choose $0 \le p_i^* \le 1$, $i=1,\dots,n$, to maximize (6).

As an example, consider the case of two prey types, and assume without loss of generality that $\frac{c_1}{h_1} > \frac{c_2}{h_2}$. This says that the per unit handling time caloric gain from type 1 prey is higher than that of type 2 prey. By differentiating (6), it is easy to show that $\frac{\partial F}{\partial p_1} > 0$, independent of the value of p_2. Thus the type 1 prey should always be included in the diet and $p_1^* = 1$. Also

$$\frac{\partial F}{\partial p_2} > 0 \quad \text{if} \quad \frac{c_2}{h_2} > \lambda_1 \left(c_1 - \frac{c_2}{h_2} h_1 \right) \qquad (7)$$

and $\partial F / \partial p_2 < 0$ if the reverse inequality holds. This implies that $p_2^* = 1$ if the condition (7) holds, while $p_2^* = 0$ otherwise. Thus, an optimal predator would specialize on type 1 prey if the encounter rate with these, λ_1, is high enough relative to the per unit time gains from type 2 prey. If λ_1 isn't high enough, then at some value of λ_1 the optimal diet is a generalist one which includes both prey types whenever they arrive. Note that there is no partial preference for either prey type; it is always optimal to take either all or none of each prey type as they arrive.

These results carry over to the case of several prey types. If the types are ranked so that $\frac{c_1}{h_1} > \frac{c_2}{h_2} > \dots > \frac{c_n}{h_n}$, then the analogous condition to (7) is:

$$\frac{c_i}{h_i} > \sum_{j=1}^{i-1} \lambda_j \left(c_j - \frac{c_i}{h_i} h_j \right) . \qquad (8)$$

The prediction is that the most valuable prey type (as defined by the ranking) should always be accepted as encountered, but as the encounter rate with it falls, the next prey item in the ranking should be included. This continues for all prey types, with the less valuable prey items being sequentially included as the encounter rates with more valuable prey types drop. Again, either all or none of particular prey types are included

in the optimal diet, eg. $p_i^* = 0$ or $p_i^* = 1$ for all i.

The above approach has a large number of limitations. Biologically, it assumes that predators can rank prey types according to their food values, and remember these rankings. The food value of a prey item is assumed to be recognized by the predator immediately upon being perceived, which ignores any recognition time necessary. The optimization criterion ignores any limitations there may be on total time available for foraging, and is taken over a short time period, rather than organism lifespan. A review of experimental tests of this model is given in Townsend and Hughes (1981). Some tests, such as Erichsen et.al. (1980), show relatively good agreement with model predictions for the situation when birds are offered different sized food items which are disguised to all appear the same. Although the diet observed was close to the optimal one, the birds portrayed a partial preference for the poorer food type, which is not predicted by the above diet model.

Aside from difficulties with the biological tests of the above model, it should be kept in mind that the mathematical aspects also present problems. The prey handling times and energy values were all assumed fixed, ignoring the variability in these within any one prey type. This might only be proper if the within-type variability is small in comparison to between-type variability in these factors. The above also doesn't analyze the full stochastic nature of the arrival process of prey, which should be looked at as a locking-counter type of renewal process with cumulative energy gains. Only the means of the random variables are considered in the above, and the optimization criterion was $\frac{E[C]}{E[T]}$, which will not in general be the same as $E\left[\frac{C}{T}\right]$. In the above, the criterion was computed at the end of a foraging bout which is a random time, rather than at an arbitrary fixed time. For the situation of Poisson arrivals, these differences do not matter, but for other models they may well be important. I discuss more on the stochastic nature of foraging later.

Patch Use

In this situation, a predator is visualized as foraging on a number of different patches which vary in the quantity and quality of prey available. These could be groups of flowers foraged by bees for their nectar, tree trunks searched by woodpeckers for insects, or dung pads visited by flies. The question of interest concerns how a predator apportions its time between the various patches so as to maximize a fitness measure. Again, the currency is assumed to be caloric gain, and the fitness criterion is taken as the net rate of energy gain.

Suppose the time taken to travel between patches is T_r, which is interpreted as a mean in this model, as are all other variables. We let t_i be the time spent searching for food in patch type i, these being the control variables. Suppose that p_i is the proportion of patches of type i, $i=1,2,\ldots,n$, $E_i(t)$ is the net energy gain obtained by searching a time t in patch i, and E_r is the locomotory cost per unit travel time between patches. Then the average time between leaving one patch and leaving the next is

$$T = T_r + \sum_{i=1}^{n} p_i t_i \tag{9}$$

and the average net energy gain during this time is

$$E = \sum_{i=1}^{n} p_i E_i(t_i) - E_r T_r \tag{10}$$

The fitness criterion is

$$F = \frac{E}{T} = \frac{\sum_{i=1}^{n} p_i E_i(t_i) - E_r T_r}{T_r + \sum_{i=1}^{n} p_i t_i} \tag{11}$$

and the objective is to choose t_i^*, $i=1,2,\ldots,n$ so as to maximize (11).

It is easily seen by differentiating (11) that if $\frac{dE_i}{dt}$ is a decreasing function, then the optimal t_i^*'s are such that

$$\frac{dE_i(t_i^*)}{dt} = \frac{E}{T} \quad \text{for all } i=1,\ldots,n \tag{12}$$

where E and T are calculated at the optimum $t^* = (t_1^*,\ldots,t_n^*)$. This says that the optimal time to leave a patch is when the instantaneous rate of net energy gain in that patch has reached the value of the overall rate of energy gain from all patches. This result, derived in Charnov (1976), is called the marginal value theorem. It implies that there will be a concentration of foraging effort to progressively fewer patches, until all patches are depleted to the average profitability of the habitat (Townsend & Hughes, 1981). If a comparison is made between habitats with different average profitabilities (E/T values), then the result implies that predators should remain a longer time in a patch with a given number of prey in the less profitable habitat than in a similar patch in the more profitable habitat.

Some difficulties with the mathematical formulation of the above will be pointed out later. A variety of other models have been constructed for patch use, including the case of a fixed "giving up time", such that a predator leaves a patch if it hasn't located a prey item there by that time (Hassell and May, 1974). In the above model the giving up time isn't fixed, but depends upon the average availability of prey over all patches. Thus a fixed giving up time would be a more reasonable assumption if the predator cannot assess the overall profitability of a site, and the time spent in a patch depends upon some innate response to each patch on its own by the predator. Another example of this is the gut-filling type of model in which the time to leave a patch depends upon how full the gut of the animal is (Cook & Cockrell, 1978). Unfortunately, the experimental tests to date do not exclude most of the above models. Hassell (1980) investigates a host-parasite situation, concluding that the data agree with the conclusions of three different foraging models, but are unable to distinguish between their assumptions. A study of heteropterans feeding on mosquito larvae (Giller, 1980) was also unable to discriminate between the gut-filling and marginal value theorem-types of models. The implication is that the models are much too simplified to be able to include the effect of complex behaviors such as variable searching efficiency and extraction efficiencies which varied with position of prey in the catch sequence.

Difficulties

Deterministic models by-in-large are the most common approach to optimal foraging theory (Schoener, 1971; Katz, 1974; De Benedictus et. al., 1978; Caraco, 1979; Craig et al., 1979; Pyke, 1979; Hixon, 1980; Sih, 1980). These models assume a fixed rate of prey arrival, fixed food value of each prey type considered, and fixed times to handle and eat the prey. Oaten (1977) has given several arguments as to why the inherent stochasticity of foraging should not be ignored. Of importance are not only that prey encounters and prey quality (in terms of food content) are sampled from a distribution, but also the predator must use this random information to determine its choice of future behavior. Other difficulties revolve around the free use of means of random variables in deterministic models, as is done in the patch use case above. Oaten concludes that the optimal behaviors deduced from deterministic models can be very poor choices when considered in a more realistic stochastic framework. In a study on bees, the model predictions were found to be completely inadequate to describe the observed foraging behavior since the effects of the variance of the bee's behavior patterns were not included (Waddington & Holden, 1979). Thus it appears a stochastic approach is essential to increase the realism of many foraging models.

Although a number of studies have included probabilistic formulations (Charnov, 1976; Sih, 1979; Taylor, 1979; Waddington and Holden, 1979), their approach is essentially a deterministic one in that they use only expected values of the relevant random variables in their models. This in effect ignores the underlying random nature of the systems. A few papers do carry out a more complete stochastic analysis (Paloheimo, 1971; Pulliam, 1974; Oster, 1976; Oaten, 1977; Caraco, 1980), though these papers mostly use expected values of the optimization criteria in determining the optimal behavior.

Oster (1976) constructs a time and energy budget model for bumblebees as a semi-Markov process. The states of the process are the behavioral roles of the predator (i.e. hive activities, feeding, loafing, etc.), the holding time distribution in each state is assumed to depend only on the most recent transition, and the optimization criterion is the expected total reward from foraging. This approach has proved useful in analyzing the structure of a bee colony (Oster & Wilson, 1978). One of its limitations however, is that risk-taking behavior cannot be considered since it is expected reward which is optimized. Later I will describe the attempt of Caraco (1980) to model risk-taking.

A More Elaborate Patch Model

As mentioned above, there are problems with the deterministic approach to patch utilization models. For example, in the above patch model, the times spent in a patch of type i, t_i, were taken fixed for any given strategy of patch use, whereas in reality they are variable. This implies that the t_i's used in the model are really expectations. But if so, then the energy gains $E_i(t_i)$ are average gains for a mean time of t_i in patch type i. The difficulty is that for different strategies with the same mean time t_i in a patch, there could be quite different expected energy gains. For example, consider a patch of unit area with exactly one prey in it, and two different foragers each of which search the patch systematically at the same speed of 1 unit area per unit time. Forager A searches half the patch regardless of what happens, while B always searches till it captures the prey, then leaves. Then A and B both search on average time $t = \frac{1}{2}$, but for A the average gain is $E(t) = \frac{1}{2}$ while for B, $E(t) = 1$. Thus to specify the model, which in this case means establishing $E_i(t_i)$, the strategy for choosing the t_i's must be known, which introduces a circularity in the model. This difficulty is pointed out by Oaten (1977), and I now proceed to describe his alternative formulation of the problem.

There are basically two stochastic elements introduced. First, prey captures are random events, with interarrival times specified by a stochastic process. Secondly, a predator doesn't know upon arriving at a patch how many prey are there, but has a prior distribution, based on past experience, on the probability the patch holds a certain number of prey. Thus a fraction q_i of patches have i prey items, where $\sum_{i=0}^{\infty} q_i = 1$. The manner in which an individual might estimate the prior distribution $\{q_i\}$ and adjust it with experience involves statistical decision theory. This aspect of the problem is not considered here, but see McNamara & Houston (1980) for the application to foraging.

The assumptions are as follows (Oaten, 1977):

(i) The predator knows only q_i = probability there are i prey in any given patch, $i = 0, 1, 2, \ldots$, and not the actual number in a patch. There is only one type of prey, and there are an effectively infinite number of patches.

(ii) Given that there are k prey in a patch and the interarrival times between prey captures are $T_1, T_2, \ldots, T_j$, $j \le k$, then $(T_1, \ldots, T_j)$ have joint probability density $f(u_1, u_2, \ldots, u_j | k) = f(\vec{u}_j | k)$, which is known to the predator.

(iii) Prey are not replaced as they are eaten, so that $T_{k+1} = \infty$ if there were initially k prey in the patch.

(iv) The time to travel between patches is τ, which is here considered fixed, but could be taken random.

(v) The decision to leave a patch is based on τ, $\{q_i\}$, the functions $f(\cdot)$, and the experience in the patch, meaning the actual interarrival times $u_1, \ldots, u_j$ and the time since last capture v_{j+1}. The predator strategy is a sequence of giving up times t_1, $t_2(u_1)$, $t_3(u_1, u_2)$, ... so that if prey have been caught at times u_1, $u_1 + u_2$, $u_1 + u_2 + u_3$, ..., $u_1 + \cdots + u_j$, then the predator will leave the patch if another prey hasn't been caught by time $t_{j+1}(u_1, \ldots, u_j)$ after the last prey capture.

(vi) A strategy of giving up times is chosen to maximize the expected number of prey eaten per unit time defined by

$$R = \frac{E[G]}{\tau + \eta E[S]} \qquad (13)$$

where G is the number of prey eaten in a patch, S is the time spent searching a patch, and η is the time spent handling each prey, here assumed constant. The value of η doesn't affect the optimal strategy, so set $\eta = 1$.

With these assumptions:

$$E[G] = \sum_{i=1}^{\infty} P[G \geq i]$$

$$= \sum_{i=1}^{\infty} \sum_{k=0}^{\infty} q_k P[G \geq i \mid k \text{ prey present initially}]$$

$$= \sum_{i=1}^{\infty} \sum_{k=i}^{\infty} q_k \int_0^{t_1} \int_0^{t_2} \cdots \int_0^{t_i} f(\vec{u}_i \mid k)\, d\vec{u}_i \qquad (14).$$

The expected search time is

$$E[S] = \sum_{i=1}^{\infty} E\Big[(T_i \wedge t_i) \prod_{j=0}^{i-1} 1_{\{T_j \leq t_j\}}\Big]$$

$$= \sum_{i=1}^{\infty} E[X_i] \qquad (15)$$

where 1_A is the indicator random variable of the event A, i.e.

$$1_A(\omega) = \begin{cases} 1 & \text{if } \omega \in A \\ 0 & \text{if } \omega \notin A \end{cases} \quad \text{for } \omega \text{ in the sample space,}$$

$T_i \wedge t_i$ = minimum (T_i, t_i), and $t_0 = \infty$. Then

$$E[S] = \sum_{i=1}^{\infty} \sum_{k=0}^{\infty} q_k E[X_i \mid k \text{ prey present initially}]$$

$$= \sum_{i=1}^{\infty} \Big\{ q_{i-1} E[X_i \mid i-1 \text{ prey present initially}] + \sum_{k=i}^{\infty} q_k E[X_i \mid k \text{ prey present initially}] \Big\} \qquad (16)$$

and letting

$$b_{ik} = q_k E[X_i \mid k \text{ prey present initially}]$$

$$= q_k \int_0^{t_1} \cdots \int_0^{t_{i-1}} \int_0^{\infty} (t_i \wedge u_i) f(\vec{u}_i \mid k)\, d\vec{u}_i$$

$$\text{for } k \geq i$$

one gets

$$E[S] = q_0 t_1 + \sum_{k=1}^{\infty} b_{1k} + \sum_{i=2}^{\infty} \Big\{ q_{i-1} \int_0^{t_1} \cdots \int_0^{t_{i-1}} t_i f(\vec{u}_{i-1} \mid i-1)\, d\vec{u}_{i-1} + \sum_{k=i}^{\infty} b_{ik} \Big\}. \qquad (17)$$

The criterion (13) is now completely specified using (14) and (17).

Oaten (1977) describes a calculus of variations procedure to specify the t_i's which maximize (13) and derives a necessary condition for a solution. For the situation in which there are only a finite maximum number of prey possible in a patch, the optimum t_i's may be computed, however there are analytical difficulties introduced by the possible non-uniqueness of the solution. The main result may be stated as: the optimal time to leave a patch, t_m^*, after the $(m-1)^{st}$ prey arrival, satisfies

$$R(t_m^* \mid \vec{u}_{m-1}) + Z = R^* \qquad (18)$$

where $R(t_m \mid \vec{u}_{m-1})$ is the conditional capture rate at time t_m given capture interarrival times $\vec{u}_{m-1}$, R^* is the optimal overall prey capture rate, and Z is a function of $(\{q_i\}, m, \vec{u}_{m-1})$ presenting the rate of future success in the patch for an optimally acting predator. The marginal value theorem of the earlier patch use model essentially ignores the Z term, and chooses t_i's to satisfy (18) with $Z = 0$. Oaten (1977) gives examples of situations in which a predator following the marginal value theorem would do arbitrarily poorly in comparison to a predator following the optimal strategy derived from (18). This arises due to the benefit a predator has in not leaving a patch immediately upon the time its rate of capture reaches the level of the habitat average, because remaining there may provide information that the patch is much richer than it appeared by prior experience.

The results of this further elaboration clearly point out the potential inadequacies of using a deterministic formulation when the underlying nature of the problem is stochastic. However, the above formulation is still not complete. The results can be readily extended to several prey types, but with the inclusion of random handling times, and finite numbers of patches so that it would be necessary to include the sampling effects on patches already visited, the analysis would rapidly become intractible. Also, the optimization criterion is the ratio of expected values, and it isn't clear that it wouldn't be preferable to use the expected value of the ratio of energy gain to foraging time. Some other potential extensions are mentioned later.

A Utility Theory Criterion

One of the criticisms that may be aimed at virtually all the foraging models developed to date is their ignorance of the variability and unpredictability of habitats. As seen in the above models, the optimization criteria are couched in terms of expected values of energy gains. This ignores the potential importance of variance in these gains. By these criteria, the same strategy would be adaptive in an environment with a constant reward value of 1 say, as in an environment which had .5 probability of reward 0 and .5 probability of reward 2. In order to include certain aspects of environmental variance, Caraco (1980) develops an approach based on utility theory, which I here briefly describe.

Suppose that B, the net energetic benefit acquired during one foraging period, is a random variable with probability density function $f(b)$. We suppose there is a real-valued utility function, $U(B)$, which specifies the utility or preference of the predator for the energy gains given by the random variable B, relative to other potential gain distributions. Here $E[U(B)] < \infty$, and suppose U, U', and U'' are continuous and $U(\cdot)$ is monotone increasing. If fitness is a concave function of net energy, then it is reasonable that U should be concave, i.e. $U' > 0$, $U'' < 0$. Then Jensen's inequality implies

$$E[U(B)] \le U(E[B])$$

and the forager prefers, in terms of utility, $E[B]$ with certainty over sampling from the distribution of B, $f(b)$. A fixed energy gain $\hat{B}$, which would give the same utility as the expected utility sampled from $f(b)$, i.e.

$$U(\hat{B}) = E[U(B)]$$

is called the *certainty equivalent*. We thus have, since U is monotone, $\hat{B} < E[B]$. This is called *risk-averse* behavior since the animal prefers to avoid the risk of doing poorly due to environmental variation in energy gains.

Alternatively, if U is convex so that $U' > 0$, $U'' > 0$, then $\hat{B} > E[B]$ and $E[U(B)] \ge U(E[B])$ and the forager is *risk-prone*. In this case, the forager prefers the risk of feeding in a stochastic environment over receiving the mean energy gain with certainty. The previous deterministic models are *risk-neutral* in that they do not differentiate between two alternative resources with the same expected rewards but different variances.

To apply utility theory, consider an environment with

n food types, each with an energy gain probability density function $f_i(b)$, $i=1,2,\ldots,n$. A resource utilization strategy would have the form

$$f(b) = \sum_{i=1}^{n} p_i f_i(b)$$

for the density associated with spending a fraction p_i of the day foraging on food type i. Here $\sum_{i=1}^{n} p_i = 1$ and the p_i's are control variables. The optimal strategy is that which maximizes the expected utility

$$E[U] = \int_{-\infty}^{\infty} U(b)\, f(b)\, db$$

subject to the constraints on the p_i's. Caraco (1980) has investigated this problem for a number of different utility functions. This allows comparisons to be made between conservative foragers who are risk-averse, and those that are risk-prone. Specific formulae can be derived to indicate how environmental variance affects the optimal strategy. A key assumption throughout this however, is that the forager knows the probability distribution for rewards for each resource. As mentioned before, if this is not assumed, statistical decision theory comes into play (McNamara & Houston, 1980).

Extensions

Foraging theories have gone a long way towards examining the potential benefits of alternative feeding strategies in a range of different ecological circumstances. It is clear that the theories have generally progressed beyond the capacity of the experimental work to date to differentiate between them. That the need for further experimental work has been recognized is observable from the large number of attempts to test the theories which are appearing in the current literature. However, there are still a wide range of theoretical questions which have not been adequately attacked. I feel that work on these would not only lead to potentially interesting theories, but also perhaps better specify the experiments necessary to adequately test the models. Below I give a list, by no means exhaustive, of the questions which I feel require further theoretical investigation.

1. Very little work has been done on situations in which foraging strategies change with the age, size, or sex of individuals. That these types of within-population feeding differences can be quite important is indicated by some experiments (Clark, 1980).

2. The question of specific requirements for a variety of different nutrients (or food types) has been addressed rather infrequently (Westoby, 1974). Quite different optimization criteria would be needed to handle this case in general.

3. Tying together foraging theory with models of predator-prey population dynamics has been attempted only rarely (Comins & Hassell, 1979). It is at this level that the coevolutionary questions implied by foraging should be addressed.

4. Some authors have derived models for foragers which include the capacity to learn about the prey while foraging and adjust their behavior accordingly (McNair, 1980). It is clear that for some organisms the ability to determine prey profitability is learned, not inherited (Jaeger & Rubin, 1982), and further work in this quite difficult area is indicated.

5. How a predator deals with a changing environment is still a very open problem. Rather than the daily time period used by most foraging models, the question of long-term optimization criteria, say over an organisms lifespan, is somewhat neglected (Katz, 1974; Craig et al., 1979). This is closely tied to problems with non-stationary environments.

6. Aside from the use of utility theory mentioned above, there is no work on the effects of the probabalistic nature of rewards on the optimization criteria. Such problems as minimizing the probability of being preyed upon by a higher-trophic level predator, while foraging, are basically not investigated (Heller, 1980). Here a full analysis of the stochastic nature of foraging is essential, extending the work of Paloheimo (1971). Criteria with constraints such as maximizing survival probability subject to obtaining a certain minimum daily intake of food are quite open problems.

7. Attempts to tie together foraging theory with biophysical energy budget requirements have been few (Powell, 1979), but are a logical next step once adequate knowledge is available on a particular organism's energetics.

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